MATING AND NESTING BEHAVIOR OF EURYSTERNUS (COLEOPTERA: SCARABAEINAE

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ABSTRACT

Mating and nesting behavior of Eurysternus caribaeus, magnus and balachowskyi *show features which distinguish them from other scarabaeines and which collectively define a distinct group of nesting behavior designated Pattern VI by Halffter (1977). These distinguishing features are: a) the "nuptial feast", a massive formation of dung balls by the female initiating nesting; b) partial consumption and abandonment of these balls by the parent(s); c) lack of ball-rolling; d) multiple nests, comprising several brood balls; e) nest care by the female; f) in some species, formation of a pair bond while nesting is in progress; g) destruction of some or all brood balls after a period of nest care (such nests are termed experimental nests); h) repetition of experimental nesting with intermittent periods of feeding until a final, or definitive nest is constructed and cared for until the emergence of progeny. Balls are made only by the female and only during nesting behavior; they are not made for feeding, although some may be consumed.*

Histological study of the ovary of E. caribaeus *suggests that attack and abandonment of an experimental nest is linked to continuation of oöcyte development during the period of nest care. Disparity between ovarial function and nest care (which represents a fault in the normal K-strategy of scarabaeines) is evidently what provokes the attack and abandonment of a nest after several days of intensive care.*

Nesting behavior of E. foedus *and an unidentified Mexican species are not like that of the species studied. Rather, their behavior is like that of certain* Onitini, *and is assignable to Group I behavior (*sensu *Halffter and Matthews, 1966).*

RESUMÉN

En este trabajo se presenta el comportamiento en la reproducción y la nidificación de tres especies de Eurysternus: E. caribaeus, E. magnus y E. balachowskyi *discutiéndose las características comunes a estas tres especies y a* E. mexicanus, *así como sus diferencias.*

El comportamiento reproductor de las cuatro expecies antes mencionadas tiene rasgos muy particulares que lo separan claramente de las pautas seguidas por los demâs Scarabaeinae, lo que llevô a Halffter 1977 a constituir el llamado grupo VI dentro patrones de nidificación de la subfamilia. Estas características peculiares han quedado confirmadas y ampliadas por este trabajo. Las mâs importantes son:

1. *Una secuencia en la nidificatión que se inicia con la formación masiva de bolas por la hembra (festîn nupcial), durante la cual o inmediatamente después ocurre la côpula; el festîn nupcial es seguido por la preparación de un nido múltiple (con varias bolas-nido) en forma de crâter que - en la mayor parte de las especies- después de un periodo de cuidados es atacado por la propia madre y abandonado (nidificación experimental) o cuidado hasta la emergencia (nidificación definitiva). Cuando se presenta nidificación experimental, al primer nido abandonado puede suceder el nido definitivo o bien varios nidos experimentales hasta llegar al definitivo, que en* E. balachowskyi *es de construcción distinta al experimental. Los nidos definitivos son cuidados hasta la emergencia de la progenie.*
2. *Sôlo la hembra hace bolas y únicamente en relación con el proceso reproductor. No hay rodaje de las bolas.*
3. *Asociamos el ataque y abandono de las bolas (basândonos en el estudio histolôgico del ovario de* E. caribaeus, *a una continuación del desarrollo y maduración de oocitos durante el periodo de cuidados del o los nidos experimentales, fenômeno que no se presenta en los otros Scarabaeinae estudiados, cuyo comportamiento incluye cuidados prolongados al nido y cese de la oviposición. Este desajuste entre el funcionamiento del ovario y los cuidados al nido (ecolôgicamente una falla en la estrategia K típica de los Scarabaeinae) es el que consideramos que provoca, después de varios días de cuidados intensivos, que las bolas-nido vayan siendo atacadas, hasta ser el nido experimental abandonado.*

Además de un estudio detallado de los cuidados y construcción de los nidos en las tres especies, el trabajo incluye una descripción preliminar del funcionamiento del ovario en E. caribaeus *y su relación con el comportamiento; la descripcîon de la formación de la pareja bisexual y del papel del macho en la nidificación; la descripción del mecanismo de côpula, incluyendo el papel de un curioso peine de sedas del âpice de las tibias anteriores del macho. También es estudiado el espermatôforo, comparándolo con los otros conocidos de Scarabaeinae, y otros aspectos del comportamiento: la oviposición, así como despliegues de agresión y limpieza, y varias pautas interesantes directamente relacionadas con la peculiar disposición de las patas medias y de las partes laterales del pronoto, que permiten un particular desplazamiento del animal boca arriba, así como el retoque y cuidado de las bolas, haciêndolas girar el animal boca arriba entre las patas anteriores y posteriores.*

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INTRODUCTION

Mating and nesting bevavior of adult *Eurysternus*, of the monobasic tribe Eurysternini, is unique in that it does not conform to described patterns for other Scarabaeinae (Halffter, 1977). Reproductive behavior of these adults does not conform well to either of the two main lines of feeding and nesting behavior, the latter being interpreted as derivations of feeding behavior. These lines are the burrowing scarabaeines (tribes Onthophagini, Oniticellini, Onitini and Coprini) and the ball-rolling scarabaeines (tribe Scarabaeini). The behavioral uniqueness of *Eurysternus* adults was pointed out by Halffter and Matthews (1966). They were unable to relate the pattern to other groups because of inadequate knowledge. Halffter (1977) created a special group, Group VI, based on his studies of *E. magnus* Laporte, *E. balachowskyi* Halffter and Halffter and *E. mexicanus* Harold, to accomodate *Eurysternus* in the evolutionary sequence proposed by Halffter and Matthews (1966). Group VI is characterized as follows: a) initiation of nesting process by elaboration of numerous balls by the female; b) partial consumption and abandonment of these balls; c) lack of ball-rolling; d) multiple nests (nests comprising several brood balls) of one or two types in the same species; e) nest care by the female alone; f) in some species, formation of pair bond while nesting is in progress; g) destruction of some or all brood balls after a period of care; h) repetition of ball construction with intermediate periods of feeding directly from an excrement mass without ball construction.

Certain morphological features of *Eurysternus* are directly related to reproductive behavior (Halffter and Halffter 1977). Both morphologically and behaviorally, *Eurysternus* is a group isolated from the two main evolutionary lines of Scarabaeinae, the burying scarabaeines and the ball-rolling scarabaeines. It originated in South America, from which it expanded into Central America and Mexico (Typical Neotropical Dispersal, *sensu* Halffter, 1964, 1976).

This paper describes in detail nidification and certain other behavior aspects of *E. caribaeus*, *E. magnus* and *E. balachowskyi*. Nesting behavior of these three species collectively shows a trend from more generalized to one progressively more complex. General aspects of *Eurysternus* behavior are covered in the description of *E. caribaeus*; only distinguishing features of the behavior of *E. magnus* and *E. balachowskyi* are considered.

Descriptions are based upon laboratory observations. We did not observe a *Eurysternus* nest in the field (most *Eurysternus* inhabit tropical forests). Halffter and Matthews' account (1966) of a nest of *E. magnus* observed in the field by H. F. Howden agrees with our laboratory findings; moreover, A. Martínez (in litt.) reports observing the nest of a South American species in the field which resembles those described here.

In all other known scarabaeines the nesting process is derived from feeding behavior. In *Eurysternus*, however, this relationship is not clear. Nidification behavior of adults of this genus is not related to their feeding behavior; moreover, it is not directly derivable from that of either the Scarabaeini or burying groups.

In all observed species (the 3 studied here plus 4 others) ball making has not been observed outside the nesting process; that is, balls are fashioned only in a reproductive context. Moreover, even though *Eurysternus* adults are capable of making balls, they cannot roll them with the legs in the scarabaeine manner; if moved at all, they are butted along with the head. The facts that balls are fashioned only for reproductive purposes, that they are produced in large number (during the "nuptial feast" and that they are not rolled by their makers clearly distinguish the behavior of *Eurysternus* adults from those of groups IV and V (Scarabaeini). Some, principally Australian Canthonines cannot fashion brood balls (Matthews, 1974); but all of them can roll pieces of excrement which are small enough and whose shape allows it. This observation would support the hypothesis that rolling was an evolutionary antecedent to ball making (Halffter and Matthews, 1966; Matthews, 1974); but it could also be considered an adaptation to special characteristics of the predominant type of dung in Australia, namely pellets of marsupials. In *Eurysternus*, however, the situation is diametrically opposed; rolling capability of adults is lacking while ability to make balls is highly developed.

For all species of *Eurysternus* known to us, adults can feed directly from a source of excrement for as long as 200 days without fashioning balls, which are made *only by the female*. Their production signals onset of reproductive activity. As Halffter (1977) points out, the nidification process in *Eurysternus* comprises 3 stages: 1) nuptial feast; 2) experimental nesting; 3) definitive nesting. In all three species studied, the female can repeat the process three or four times under conditions which presumably preclude ecological restrictions. These species have exceptionally long adult lifespans for Scarabaeinae, which may exceed two years.

Eurysternus Behavior

E. caribaeus (Herbst)

All material upon which the following observations are based were field-collected in two neighboring localities in the Lacandon rain forest, Chiapas, Mexico: Chansayab-Lacanjá and Bonampak. *E. caribaeus* occurs from Formosa, Argentina northward to Honduras (Halffter and Halffter, 1977). All material studied came from more northern populations which could represent a distinct species or subspecies neither of which was formally decided by Halffter and Halffter, (1977) because of a lack of sufficient data on the intraspecific variation of the South American *E. caribaeus*. Distinctive features of populations from which study specimens came are the almost uniformly dark dorsal and ventral surfaces (some specimens show the spotted appearance of typical *E. caribaeus*) and somewhat shorter average length.

Elaboration of balls, the nuptial feast. – The nuptial feast begins suddenly with rapid construction of a large number of balls by a female. We suppose that its initiation is linked to developmental state of the ovary. *E. caribaeus* females construct two to four balls within three or four days after emergence when oöcytes have barely begun to develop. Nevertheless, construction stops very quickly.

Once the nuptial feast has begun, the female is soon joined by a male. If a male does not arrive, the process is interrupted; we did not observe a nuptial feast completed by females isolated from males. Moreover, except for premature initiation of nidification (as mentioned above) females do not make balls if they are maintained in the absence of male contact.

Balls are made rapidly during the nuptial feast in the following fashion by *E. caribaeus* females; work begins in the lower part of the dung mass using the head and front tibiae while the middle tibiae are extended upward or rested on the dung and the posterior tibiae are rested on the ground or dung. A female enters a dung mass and separates a dung ball (Fig. 1) using the middle legs like oars to move herself in a manner unique to *Eurysternus*. From an upside-down position the middle legs are moved anteriorly beneath the dorsal surface while the tips of the tibiae are planted. Thus, the tips serve as support points for forward movement of the entire body. Such movement of the tibiae is permitted by the rounded shape of the pronotum (Halffter and Halffter, 1977). This "rowing" movement has also been observed in females of *E. magnus* and *E. balachowskyi*.

Once the ball is separated, the female begins another from within the cavity resulting from construction of the first, or to one side of it. Formation of each ball takes about 50 minutes; females of all three species, make balls continuously. Nevertheless, interruptions of up to several days can occur, after which a female resumes ball fabrication. Such interruptions cause marked variation in number of balls produced and duration of ball making (see Table 1).

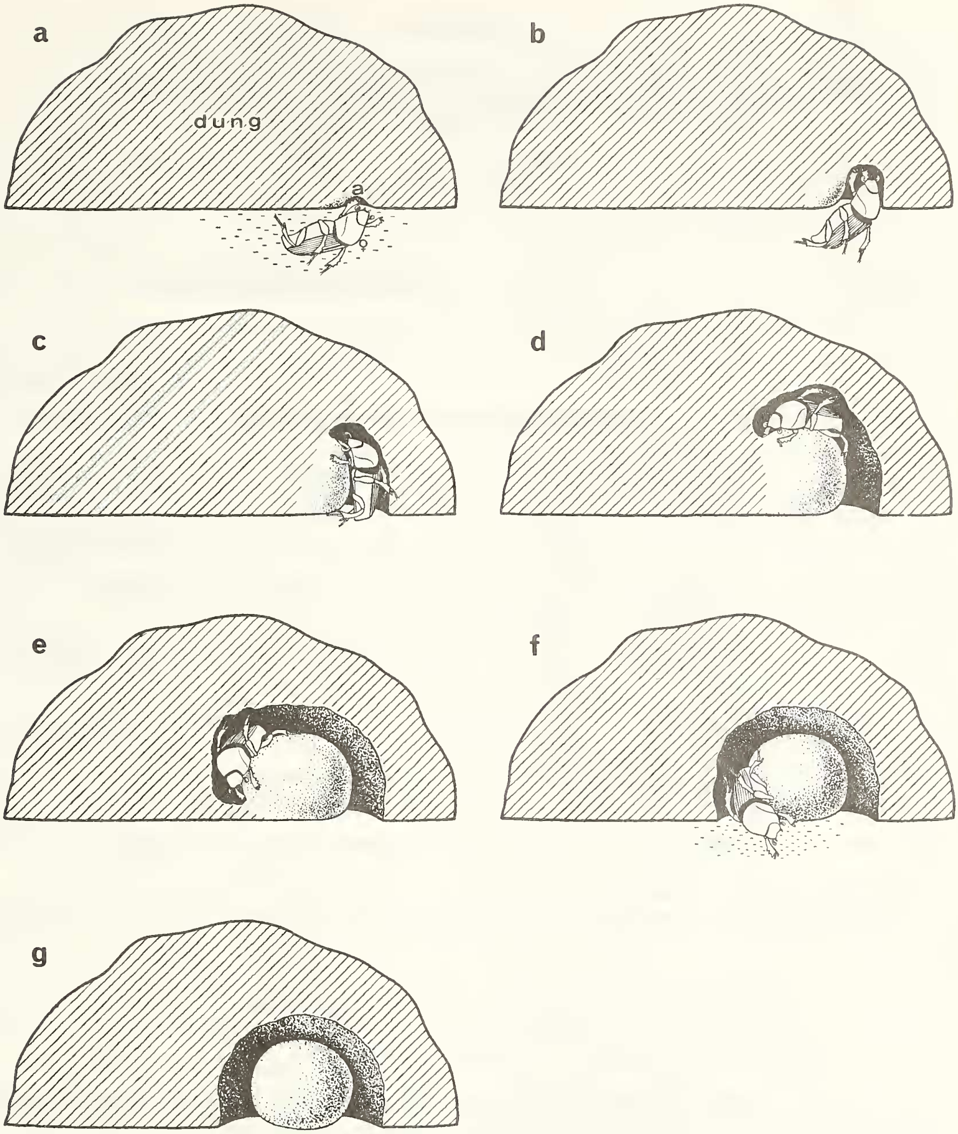


Fig. 1. *Eurysternus caribaeus* Hbst.. *a-g*: successive stages in the elaboration of a ball during nuptial feast

Balls produced during the nuptial feast are not exactly spherical nor uniform in size. Although eggs may be laid in from two to five of them by females of *E. caribaeus*, most balls are without eggs.

When a female has been deprived of male contact, she may begin ball making but the number does not exceed four. Production of many balls requires presence of a male, as does completion of the nidification process.

During the nuptial feast, both sexes of all three species eat directly from the dung source or from balls fashioned by the female, most of which are partially consumed and later abandoned.

TABLE I

COMPARISON OF ASPECTS OF NESTING BEHAVIOR OF THREE SPECIES OF *Eurysternus*

ASPECT	SPECIES OF Eurysternus		
	E. caribaeus	*E. magnus*	*E. balachowskyi*
A[1]	16- 94, $\bar{x}$ = 34.5	9- 11, max.= 17	max.= 55+ 31- 50, during expt. nesting.
B[2]	7- 69, $\bar{x}$ = 29.8	12- 28	60- 90
C[3]	65- 80	not observed	not observed
D[4]	13- 82	1	continuous
E[5]	2- 6, $\bar{x}$ = 4.2	3	
F[6]	38- 53	25- 26	40

[1] Number of balls made during the nuptial feast.

[2] Duration of the nuptial feast (in days) from the making of the first nesting sequence, during which ball-making may continue interrupted or not.

[3] Duration of copulation, in minutes.

[4] Period (in days) between the end of the nuptial feast and beginning of next nest.

[5] Final number of balls in the definitive nest.

[6] Duration (in days) of the definitive nest.

Ovary development and behavior. – As is true for females of all Scarabaeinae (Halffter and Lopéz, 1977), the ovary of a *Eurysternus* female consists of a single ovariole (on the left side). The ovaries of *E. caribaeus* females possess two characters which are unusual to scarabaeines, particularly to those with advanced nidification: 1) the adult emerges with a completely developed germarium and 2) oöcyte maturation begins very soon and is rapid. It appears contradictory that even when a female is provided necessary male company (in a terrarium), the nuptial feast does not begin for at least 20, and as many as 50 days thereafter. Moreover, an additional delay results from the nuptial feast itself and periods during which it may be interrupted. Why there is such a long delay in egg production in spite of the ovarial condition of a newly emerged female may be explained by a prolonged period of vitellogenesis, which is much longer and morphologically more elaborate than in any of the few other scarabaeines females studied (Fig. 2).

The fecundity of *Eurysternus* females more nearly approaches that of a scarabaeines with primitive nidification, such as *Onthophagus*, than that of one with more advanced nidification. This high fecundity may explain destruction and abandonment of experimental nests to begin a new nest (*E. caribaeus*, *E. balachowskyi* and *E. mexicanus*). High fecundity is perhaps also the explanation of frantic formation of balls during the nuptial feast, most of which are not used. In addition, the following ecological fact may obtain: the high number of balls may serve to compensate for losses through robbery by ball-rolling scarabaeines, losses which should be important during fierce competition for excrement within tropical forest.

Upon emerging, the germarium of *E. caribaeus* is completely developed (Fig. 2-a) but does not contain developing oöcytes. Three days after emergence, two developing oöcytes and two nascent ones are at the base of the germarium (Fig. 2-b). Such a rapid development of oöcytes is completely out of the ordinary for scarabaeines. Nineteen days after emergence, still before beginning the nuptial feast, the ovariole bears 6 oöcytes (Fig. 2-c), within the most mature of which are lipid globules while at the same time the germarium is reduced.

The nuptial feast begins a few days later when the ovariole contains a series of oöcytes of which the first ones are mature. During the feast (the function of which appears to be attraction of a male) copulation can occur at any time. Figure 2-d illustrates an ovary of a female during the nuptial feast immediately after copulation: four oöcytes contain large quantities of granules; the fifth and sixth are forming. During this stage as many as eight oöcytes in various stages of development are distinguished.

If a male is present, the nuptial feast develops; if copulation occurs, some days later (depending upon the state of maturation of the ovary) *nidification continues.*

We suppose that destruction and abandonment of brood balls in experimental nests are due to continuation of oöcyte formation. Whatever the mechanism is in other scarabaeines (Halffter and Lopéz, 1977) which, in concert with ovarial development, determines female behavior and which, in turn (according to the phase of reproductive behavior) inhibits the ovary, it does not function in *Eurysternus*. Unlike other groups with complex nidification (Groups II, III and V, Halffter, 1977), the ovary of a *Eurysternus* female continues oöcyte production, she continues ovipositing in new brood balls and simultaneously attacks or abandons those which were being cared for.

We suppose that these continuous processes end with completion of the first series of oöcytes, at which time the female ceases destruction and initiates care of what will be the definitive nest.

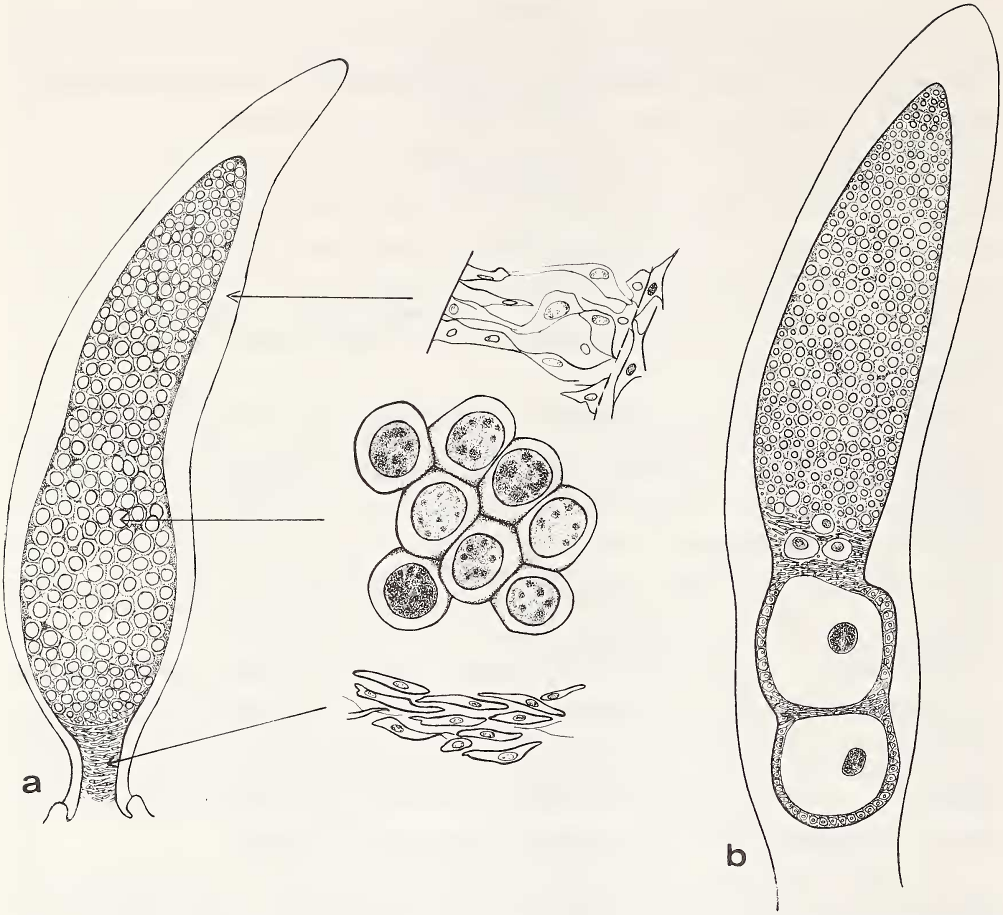
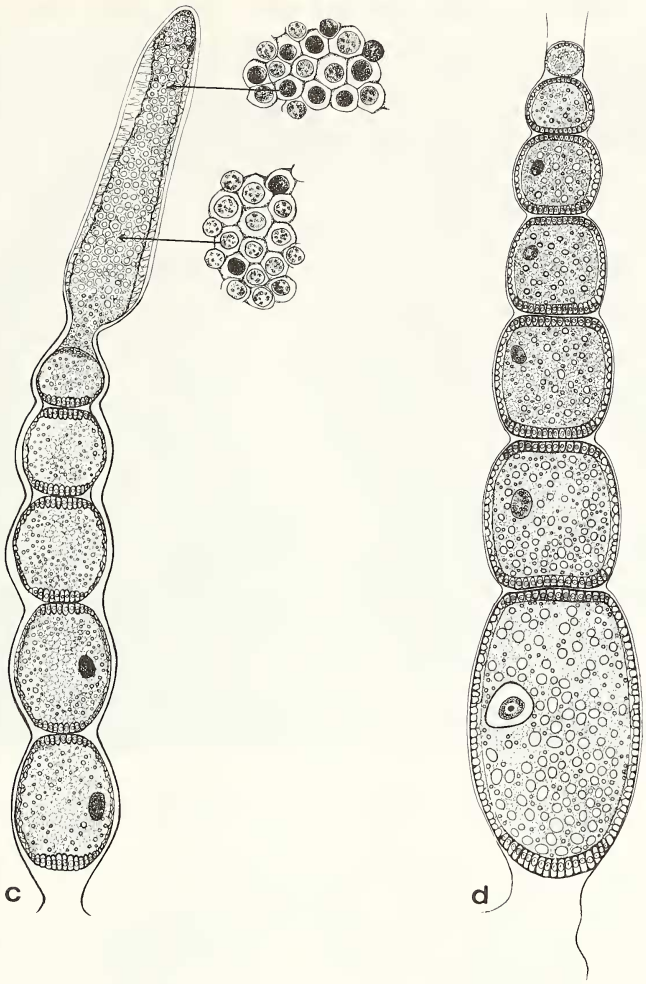


Fig. 2. Development of ovary in *Eurysternus caribaeus* Hbst.*a:* One day after emergence, there is no differentiation in germarium formed by cells with very pigmented nucleus (trophocytes) and cells with nucleus less pigmented (oöcytes) - see detail; other details indicating the tunica propia and the inner and outer layers, as well as the mass of prefolicular cells; *b*: three days after emergence - two oöcytes in vitellogenesis, several in initial process of development in the base

During care of the definitive nest (Table 1), a new series of oöcytes matures in females of *E. caribaeus.* Toward the end of care, the ovary resembles that observed in the midst of the nuptial feast. Copulation may occur at this time and a second nidification process begins immediately after termination of the first (even before emergence of offspring) without an intermediate feeding period.

Variability of duration of the nuptial feast as well as timing of copulation explains why eggs are in some (but few relative to the total) balls of the nuptial feast of *E. caribaeus.* This indicates that the first oöcytes can mature before the end of the feast, at least under laboratory conditions. We do not know if in the field, under conditions of intense competition, prolonged nuptial feasts are possible without balls being robbed.

Formation of the bisexual pair. – In all three species studied, a male joins a female during the nuptial feast in the midst of ball formation. As in *Phanaeus*, (Coprini; Halffter, Halffter,



of germarium; *c*: 30 days after (before the beginning of nuptial feast - development of the vitellarium, in the germarium, trophocytes tend to concentrate in the apical extreme; *d*: vitellarium 45 days after emergence, in the middle of the nuptial feast, immediately after copulation - the more mature oöcytes are close to oviposition.

and Lopéz, 1974) but unlike Scarabaeini, a female's activity attracts a male. In *Eurysternus*, formation of brood balls acts as an attractant for a male.

In *E. caribaeus*, the pair remains intact only during the nuptial feast. In *E. magnus* and *E. balachowskyi*, pairing is maintained through experimental nidification. Most females of all three species are alone during preparation and care of the definitive nest. Nevertheless, in *E. caribaeus* we have seen copulation in a definitive nest during the period of care. This copulation is part of the second nidification process to follow and likely owes its occurrence to conditions within the terrarium, which prevent the male from leavingy and favor encounter with the female during maturation of the new series of oöcytes. In the field a female may encounter another male upon beginning a new nuptial feast after emergence and dispersal of her offspring and an intermediate feeding period.

Copulation. – Normally in each reproductive cycle a single copulation occurs during the nuptial feast (among the balls or at the side of the dung mass, Fig. 3). It may also occur a second time during care of the definitive nest or during the last phase of care of the definitive nest in *E. caribaeus*, but when it does it results in abandonment of the nest and initiation of a new nidification process. In *E. caribaeus*, the male approaches the female from behind and mounts her while tapping her elytra with the front legs while supporting himself on the ground with the hind legs. The middle legs are held extended dorsolaterally. Meanwhile, the female remains quiet and continues feeding. In a few minutes, the male has situated himself horizontally over the female (Fig. 3) while grasping her abdomen with his back legs, the tibiae of which are curved to facilitate hanging on. (To different degrees, this curvature of the hind tibiae is a secondary sexual feature of all male *Eurysternus* studied). Meanwhile the middle legs remain extended while the anterior legs softly caress the pronotum. At this moment, the aedeagus is extended but not yet engaged in the female genital opening. The female, which up to now had remained quiet, begins a series of movements which result in the pair being upside down or lying on one side. The male remains strongly attached while continuing to caress the female. When the female ceases movement, the male introduces the aedeagus and inserts the internal sac.

The female remains quiet 30 to 45 minutes before resuming her movements. The male remains astride her but disengages the internal sac and withdraws the aedeagus. The female finally succeeds in separating herself from the male using strong movements. Observed copulations have lasted 65 to 80 minutes.

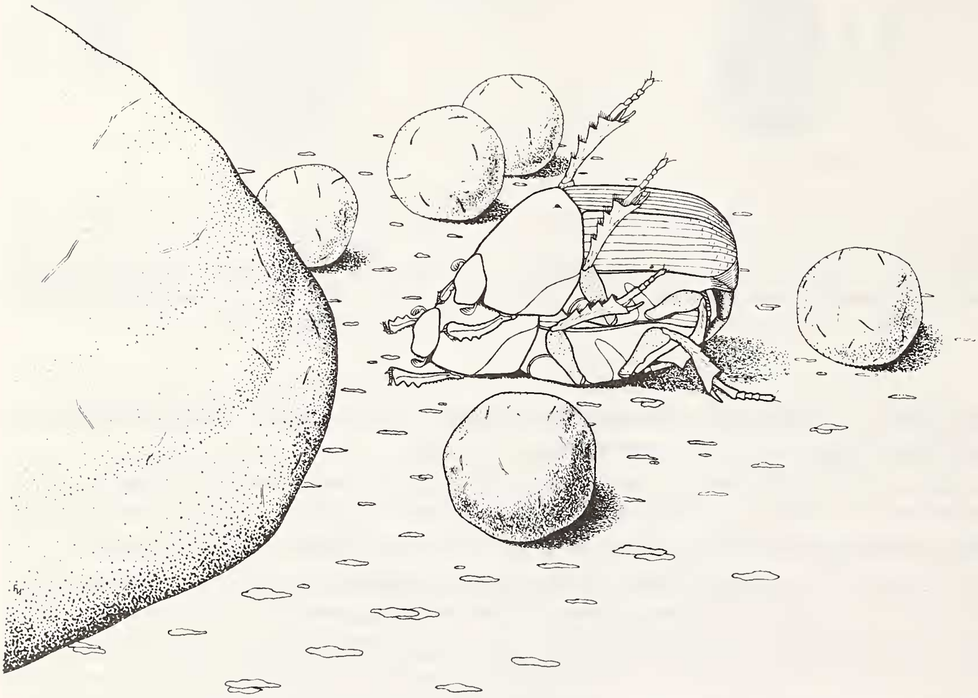


Fig. 3. *Eurysternus caribaeus* Hbst. Copulation during nuptial feast.

Fig. 4. *Eurysternus caribaeus* Hbst. Spermatophore immediately after its deposit in vagina.

Halffter and Halffter (1977) describe a curious lobe bearing a comb of setae on the apex of the male tibia. They believed the structure to somehow be related to the fact that a male sometimes cares for brood balls; that is, that the combed lobes were used to clear or otherwise retouch the brood balls. Such now appears not to be so. The structures appear to be important to *stimulation of a female* during copulation. This is the first structure of scarabaeines directly and clearly related to sexual stimulation. Although similar stimulation appears characteristic of scarabaeines in general, *Eurysternus* is the only group with a special morphological modification which complements it, although males of several *Onthophagus* have a tuft of setae at the apex of the anterior tibia.

In *E. caribaeus* the spermatophore is a very long, translucent tube containing spermatozoans (Fig. 4). The ovoid shape of the compacted tube suggests a circular movement during ejaculation with a gradual retraction of the free tip of the internal sac. This movement occurs in spite of the spines of the internal sac which contact the sclerites of the wall of the vagina. The few spermatophores known for other species have different forms indicating a different movement during deposition (Heymons, 1930; Huerta, 1977; Halffter and Lopéz, 1977).

The spermatophore occupies more than half the vagina. Form of the spermatheca, spermathecal muscle and spermatozoans suggest that insemination follows a process like or very similar to that observed in *Phanaeus* (Halffter and Lopéz, 1977).

When copulation is complete, the crater-like nest is not immediately begun. Since copulation can occur at any time during the nuptial feast, the time between copulation and crater construction varies. Moreover, some balls made during the nuptial feast are provided with eggs. Thus, relatively rarely, copulation and complete maturation of some oöcytes begins so early that some balls receive eggs during the nuptial feast. The chances that these eggs later develop are remote since most are destroyed by the parents or left uncared for.

Nidification. – The nuptial feast is followed by experimental nesting which is not as distinct an event in *E. caribaeus* as in *E. balachowskyi.*

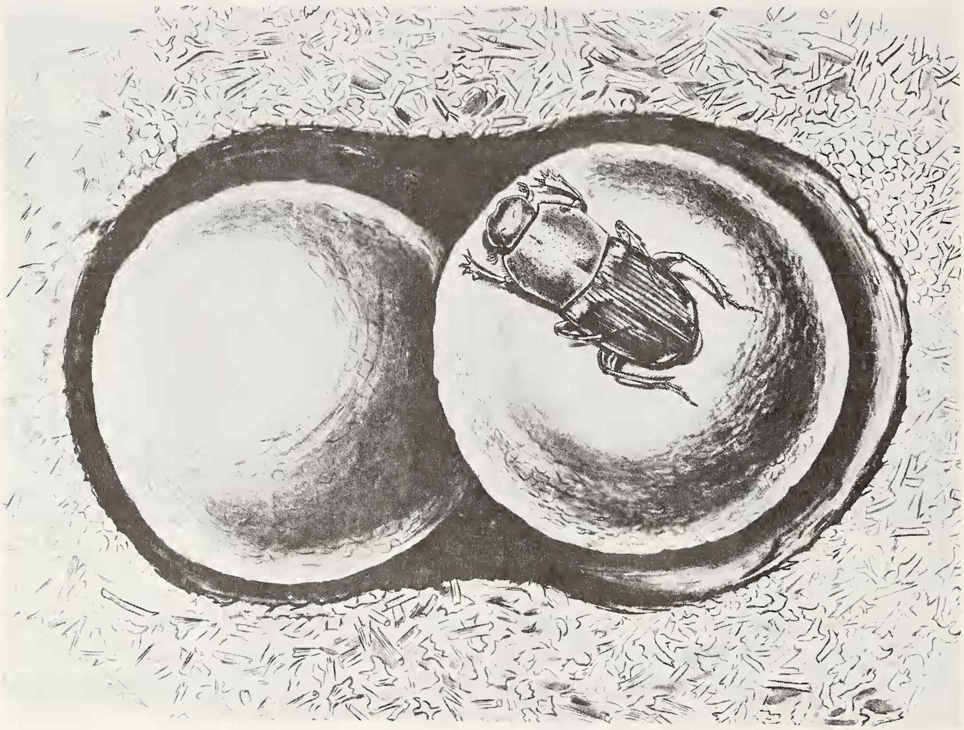


Fig. 5. *Eurysternus caribaeus* Hbst. Female caring for definitive nest.

In *E. caribaeus*, experimental nesting is represented by those beginnings of craters and brood balls which are abandoned by the female. Experimental nests occur in 65% of observed cases; 35% of observed nidification by *caribaeus* included no experimental phase.

Definitive nesting.. – Preparation of a definitive nest is strictly linked to state of the ovary; its timing corresponds with maturation of the last oöcytes of a single series. (Recall that the life of a female may, however, include several series). We believe that nest destruction is inhibited by and continuous care maintained by, an interruption in maturation of oöcytes. Conversely, nest care behavior acts as a temporary inhibitor of oöcyte maturation. Evidently female behavior changes during definitive nesting such that ball destruction and abandonment are not manifested.

In *E. caribaeus*, nidification (definitive or experimental) begins 13 to 82 days after the end of the nuptial feast. This variation is due to differences in the timing of copulation and maturation of oöcytes.

The definitive nest of *E. caribaeus* is a crater dug by the female, beneath several previously fashioned balls; several other balls may be pushed into the crater. Initially, the crater contains seven to 12 (average 8.7) balls, of which two to six (average 4.2) remain in the completed nest. The latter are provided eggs and an external layer of soil.

To prepare the definitive nest a female uses the last balls made during the nuptial feast. They receive final modelling, which results in their being larger than balls constructed previously (seen also in *E. magnus*). The balls are slightly increased in diameter as the nest develops. The average diameter of balls containing eggs is 23.9 mm; that of balls containing larvae, 24.7. This increase is produced by the larva by its continual repair to the internal surface using its excrement without breaking the wall and the action of the mother on the outside surface.

In the definitive nest, brood balls are carefully modelled and covered with a layer of soil, which often binds two to four balls into a single, compound structure (Fig. 6).

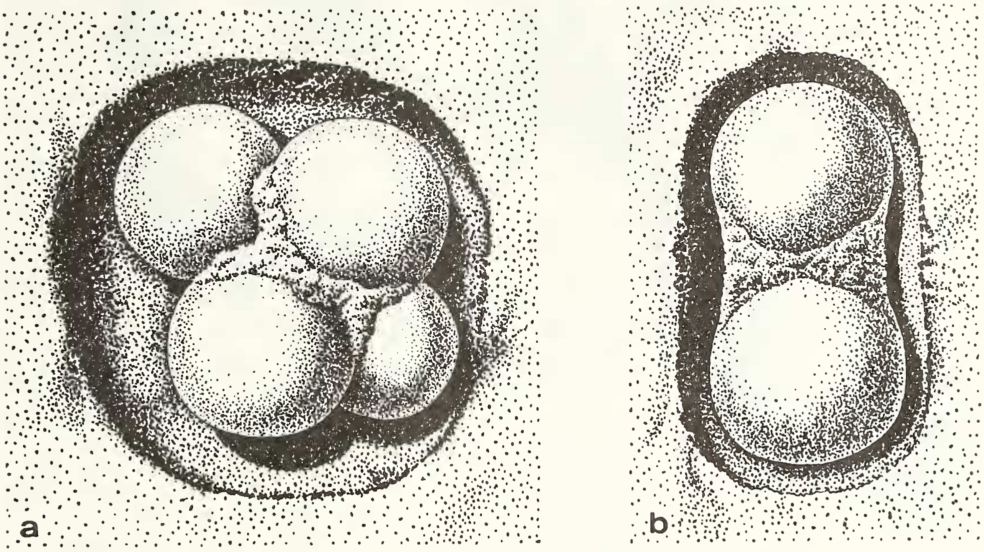


Fig. 6. *Eurysternus caribaeus* Hbst. Types of definitive nest. Observe the union of brood-balls with soil.

Nest abortion, or cessation of care and abandonment or attack of balls occurs before the soil layer is added. Protection of the soil layer is ended when the larvae reach the third instar.

Nest formation is not rapid since it includes much modelling and remodelling and spaced oviposition. Thus, a single nest may include balls with eggs and other with larvae in all stages of development. Toward the end, development stages among progeny tend to become equalized.

As a nest develops, a female may depart for several hours to feed, but she returns. She cares for brood balls in the definitive nest until emergence of new adults. A male does not participate in nest care; normally he is not present. The nest crater can be to the side of the dung mass from which the brood balls were extracted or beneath it. If beneath, the nest crater is hemispherical. Definitive nesting lasts 38-53 days, during which a female maintains constant care. If copulation occurs during the care period, within a few days after emergence of progeny the female begins a new nesting cycle by initiating a new nesting process.

Lapse of time between two nests depends upon whether or not copulation occurs during care of the definitive nest. One female, which had copulated 20 days previously, began a new nidification beneath the nest she was caring for. At the time the nest balls contained pupae, whose care she abondoned (Fig. 7). The new nest was not finished.

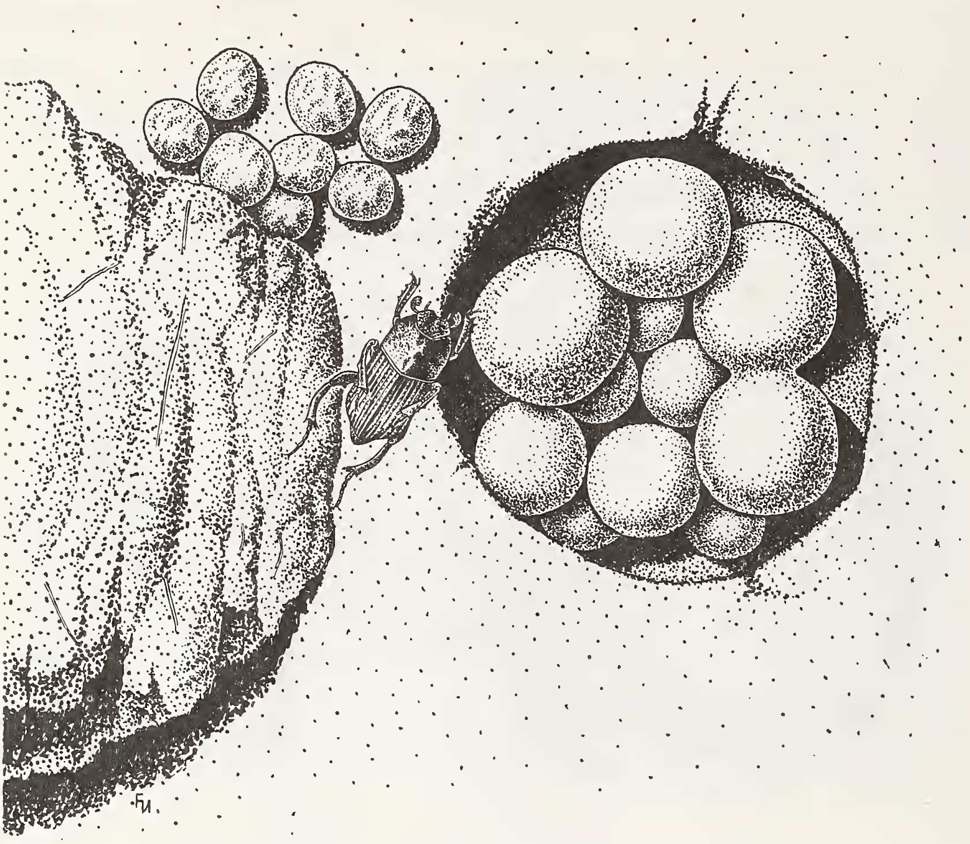


Fig. 7. *Eurysternus caribaeus* Hbst. Exceptional case: in same crater two nests were superposed.

Eurysternus magnus Laporte

Material upon which the following observations are based was collected at Lagunas de Montebello, Chiapas, an area of pine – *Liquidambar* forests at 1400 m near the Guatemalan border.

Cleaning. – The system of self-cleaning by *E. magnus* adults is probably used by those of the other two species studied. Dorsal surfaces of the elytra are cleaned with the middle tibiae and tarsi; apices, with the hind tarsi. All *Eurysternus* adults bear numerous ocellate punctures, each with a central seta, particularly on the pronotum. These punctures easily collect dry excrement and dirt, which normally cover part of the entire dorsum. "Dirty" appearance coupled with normally obscure brown or black coloration results in a rather striking cryptic coloration. Adaptiveness of the cryptic appearance is enhanced behaviorally by the habit of remaining motionless (thanatosis) such that *Eurysternus* adults are exceedingly difficult to see in their natural surroundings. Presumably this cryptic coloration offsets increased vulnerability of these beetles resulting from the fact that they do not burrow like almost all other scarabaeines.

Ball construction, nuptial feast. – We have observed *E. magnus* adults feeding directly from dung for as many as 190 days. Some enter the dung mass superficially to eat. The nuptial feast begins suddenly as in *E. caribaeus*. Number of balls prepared varies from nine to 11; Maximum observed was 17. These balls are eaten, changed in position, destroyed and remodelled and only a small portion is used for nesting.

Balls are separated from the margin of the dung mass in contact with the ground. The female may separate the ball in an upside-down position using the front legs (cf. *E. caribaeus*). The margin of the dung mass presents concavities in places where balls have been separated. Balls are constructed rapidly but with little care until the dung mass is exhausted. Rhythm of construction is not uniform but is continuous. Fresh balls are only roughly spherical, not smoothed over and with an approximate diameter of 15 mm. During intensive ball-making, some are moved randomly on occasion (up to 9 cm) by pushing with the head and forebody while planting the front and hind legs. Pushing is not continuous, but rather is achieved by a series of butting motions.

Nesting. – Definitive nesting occurs from 12 to 28 days after beginning the nuptial feast. Females of *E. magnus* do not construct experimental nests. The nuptial feast is followed by the excavation of the nest crater, which is not destroyed, as are 65% of the nests of *E. caribaeus* and all nests of *E. balachowskyi*.

A nest is begun with balls from the nuptial feast, which are remodeled superficially by adding excrement. The crater is dug beneath three of these balls; excavation requires a day. The finished crater is shallow, circular and about 5 cm in diameter (diameter of the rim is somewhat less than that of the floor). The day after finishing the crater, about three more balls are pushed into it. Thus, at first the nest contains more balls than will be converted into brood balls, generally three (Fig. 9). The extra balls are used for food, to finish the brood balls or simply taken apart.

A few hours after finishing the crater, a female models or retouches the balls and begins oviposition even though all balls will not receive eggs. Two days after nesting is begun, a female begins adding soil cover to the balls; this activity lasts as long as seven days. After oviposition and covering are completed, brood balls are cared for continuously throughout development of offspring.

As the brood balls are cared for, their positions are changed continously by pushing or, in an upside-down position, by making them turn using the front and hind legs from beneath or from the side (Fig. 8). The front tibiae are used to retouch and smooth their surfaces. Balls are cared for alternatively and continuously and are not joined with soil as in brood balls of *E. caribaeus* (Fig. 9). Although a ball may be attacked, the nest is not destroyed.

Once we have seen a male caring for brood balls, changing their position frequently while the female continued to fashion balls from the nearby dung mass until it was exhausted. Some of these balls were eaten, others simply abandoned. A male of *E. magnus* remains with a female during nest formation and during part of the period of care. Rarely a female and much more frequently a male may, for a short time, move to feed from a nearby dung mass before returning to the nest.

As in *E. caribaeus*, brood balls are increased in size during development. Balls constructed for the nuptial feast have an average diameter of 15 mm when formed from the dung source.

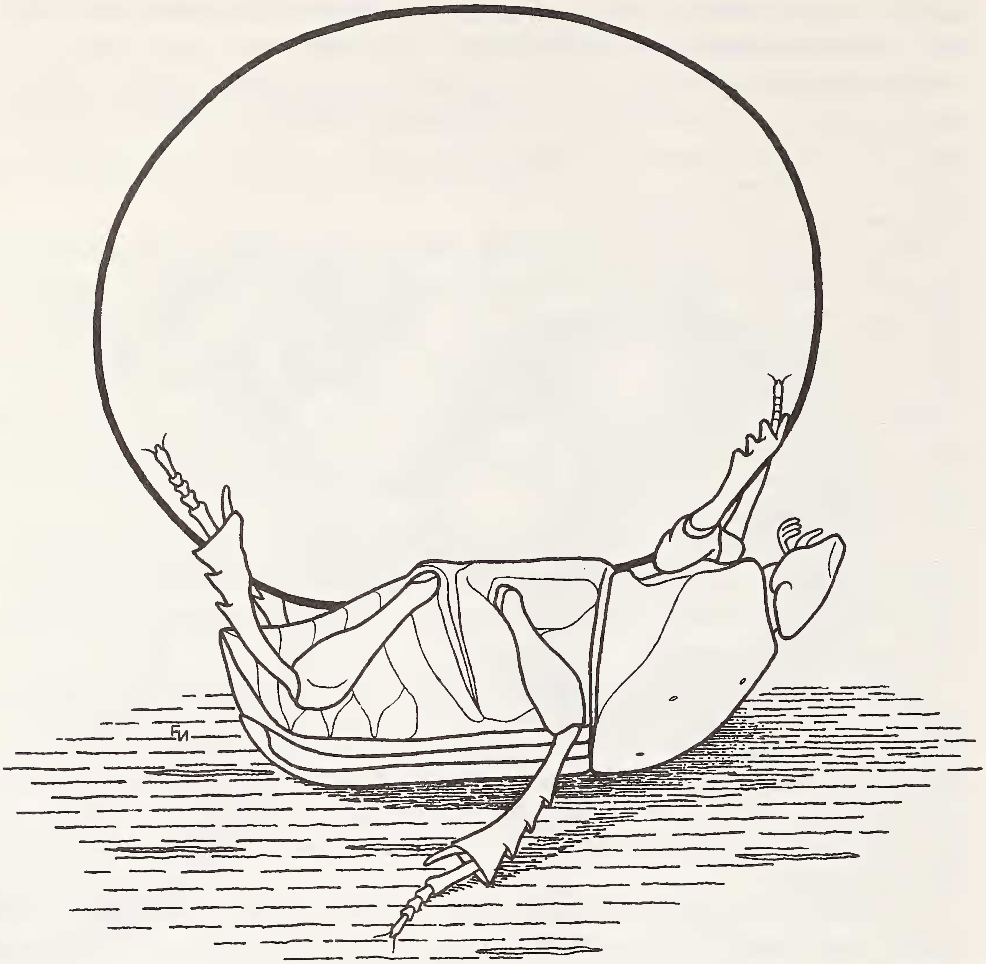


Fig. 8. *Eurysternus magnus* Laporte. Female turning nest ball in interior of crater.

After being remodelled (using fragments from other balls or from the dung source itself) the diameter exceeds 18 mm. The brood balls have an average diameter of 21 mm.

Subsequent nests of *E. magnus* are not constructed as rapidly as are nests of and *E. caribaeus*. About 170 days elapse between emergence of adult progeny and initiation of a new nuptial feast.

Oviposition. – We have observed oviposition in detail only by females of *E. magnus* but believe it must be similar in *E. caribaeus* and *E. balachowskyi*. Using her front legs, a female forms a hole in a prepared ball into which she enters almost completely and remains about five minutes. Afterwards, she withdraws, turns, and introduces her abdomen. For another five minutes, the hind legs are moved up and down while the middle legs rub the sides of the body. Oviposition is in the bottom of the cavity. The female then collects dung from the same ball to close the egg cavity using the front legs to work it into the opening as she turns around it. Oviposition lasts 25 minutes, after which the egg remains in a small central cavity.

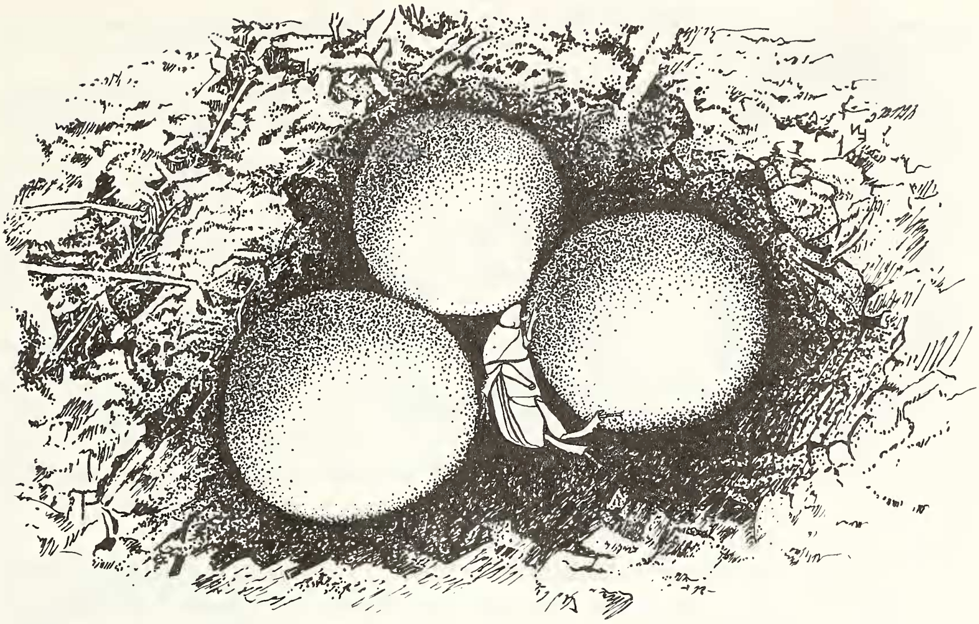


Fig. 9. *Eurysternus magnus* Laporte. Definitive nest. Observe balls are not united by soil.

Eurysternus balachowskyi **Halffter and Halffter**

Observations are based on material from French Guiana (see Halffter and Halffter, 1977).

Ball-making, nuptial feast. – The nuptial feast of adults of this species is the largest (to 55 balls) and longest (to two or three months) of those species studied. Many of the balls are abandoned or partially consumed. No eggs have been found in nuptial feast balls. Although ball making is not suspended for more than a few days its rhythm is not uniform. Thus, for some days a female makes no balls, but on others she may make several.

Balls can be separated from the upper part of a dung mass and from there rolled to the ground. A female may work right side up or upside down, but either way she separates excrement *in small bits* which are molded into a ball. The front legs are used to incorporate and press the dung while the back legs, by making the mass turn between them, give the ball its spherical shape. The middle legs remain free to either support the body or to move it with oar-like movements as described for *E. caribaeus*.

Ball-making by *E. balachowskyi* females differs from that of *E. caribaeus* in that, rather than separating an entire ball from a dung mass in a single operation, it is gradually built up by fragments added to the growing ball by the front legs. Completed balls either accumulate to one side of the dung mass or they are pushed short distanaces. They are not exactly spherical; the lesser diameter varies between 15 and 18 mm while the greater varies between 15 and 20.

Some of the balls are retouched at one side of, or some distance from the dung mass. As balls are moved, they are grouped; some of each group are retouched. Some smaller balls are combined with larger ones, upon which the beetle perches as it pulls and incorporates the smaller with the front legs. Debris produced by retouching include small pieces of dung, small balls, including some already worked. The front legs press and smooth the surface of the ball;

later a thin layer of soil is added. Retouching includes spinning the ball with the front and back legs while the female is upside down.

At the end of the nuptial feast, some retouched balls receive eggs. The first oviposition begins the experimental nesting phase; during the nuptial feast (in the strict sense) no balls receive eggs.

Oviposition is followed by formation of a nest crater. In the other two species, crater excavation precedes or coincides with oviposition.

Experimental nesting. – For approximately 60 days after the nuptial feast, a female oviposits in a number of balls and constructs about three successive craters where the balls are placed and cared for a few days before they are attacked, partially consumed and abandoned.

In contrast to the other two species, the *female continues ball-making during experimental nesting (31 to 50 additional balls) if excrement is nearby*. Undoubtedly, this prolonged process of ball-making is related to destruction and abandonment of experimental nest craters. The nuptial feast, with its characteristic elaboration of balls, overlaps with experimental nesting, with its oviposition and formation of nest craters. This overlap we attribute to a continuously active ovary, which by not ceasing activity, fails to produce the metabolic signal that the nest should be cared for and ball-making ended.

Balls made during experimental nesting and at the end of the nuptial feast have two possible fates: some are abandoned, whether or not they contain eggs; others are taken apart and partially eaten, whether or not they contain eggs. Some eggs in balls removed from terraria develop; others do not.

Preparation of the nest crater is very similar to that of *E. magnus* and *E. caribaeus* females. Some balls are provided with a thin soil covering. As for *E. magnus*, the male of *E. balachowskyi* often remains with the female and can participate in care of the brood balls. Remodelling of the balls in the nest crater and their care is exactly as described for *E. magnus*. Within a few days, four or five well worked balls are in the nest crater; of these, three large ones finally remain and (rarely two) are completely finished and with eggs and a thin layer of soil. They are cared for by the female. About two days later, one of the balls is eaten by one of the parents, but the female continues caring for the others for approximately six days. During this time the female does not leave them but attacks and partially consumes some of them. Eight days after the first attack, most balls have been damaged by the parents and the nest crater is abandoned.

During the period a male or female may eat from a nearby dung mass (the attack is not occasioned by hunger) and, moreover, the female may make other balls which are pushed into the crater and ultimately destroyed. Some balls may by chance survive the attacks and the egg continues its development.

After a period of direct feeding, experimental nesting is repeated, generally three times, with the consequent abandonment of the nests.

Oviposition is similar to that by *E. magnus* females. Each egg is in a chamber near the upper pole of the brood ball closed by a plug of loosely compacted grass fibers. Oviposition can occur either on the surface, after massive ball-making, or in the nest-crater.

Definitive nesting. – The definitive nest of *E. balachowskyi* adults is different from experimental nests in both how it is made and in its final structure. Of the last balls made, two are separated for definitive nesting. This separation begins definitive nesting and occurs about five months after beginning of the nuptial feast and about two months after the first oviposition and experimental nest. The two balls selected have diameters exceeding 27 mm; they are placed

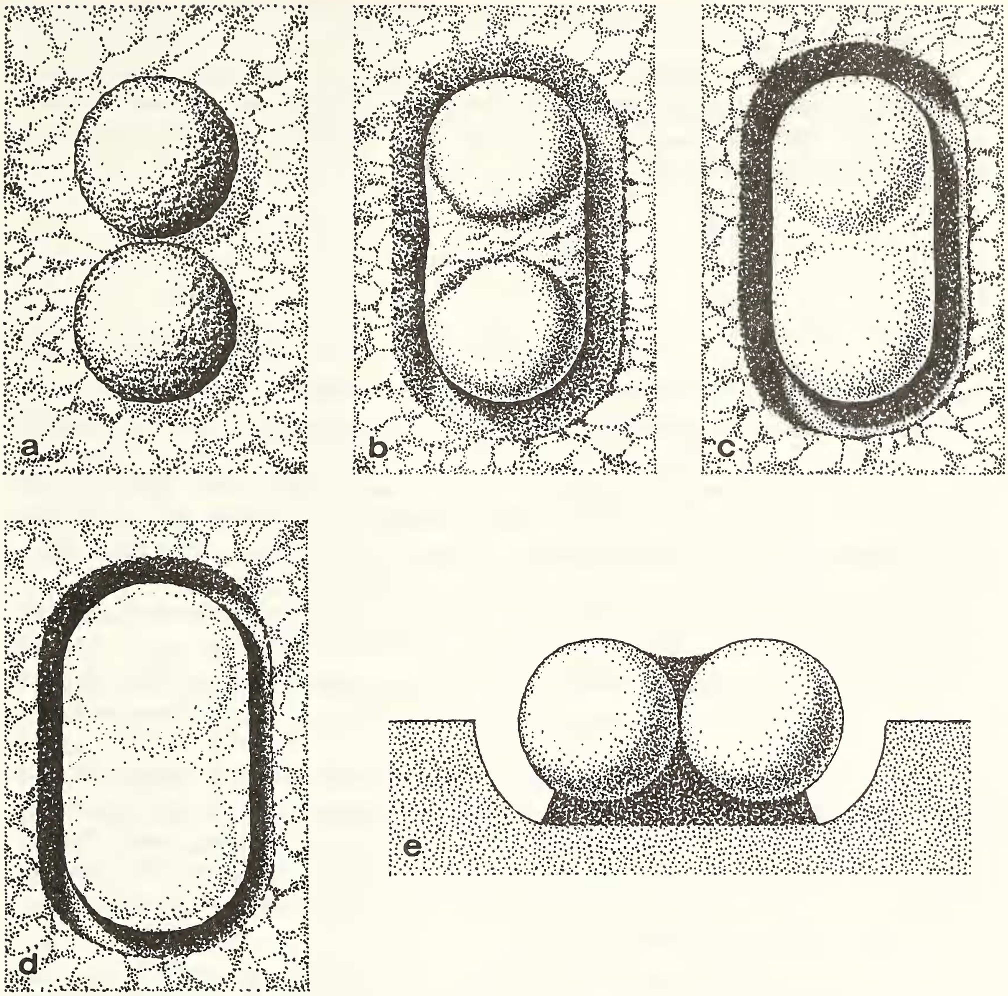


Fig. 10. *Eurysternus balachowskyi Halffter and Halffter.a-d*: stages in formation of definitive nest in dorsal view.- two brood balls united with soil and peripheral groove deepens; *e*: definitive nest cut transversely.

on the surface in contact with each other (see Halffter, 1977, Fig. 12) 15 to 20 cm from the dung mass and covered with soil. The female then excavates a groove around them (see Fig. 10) which is enlarged until the balls are in contact with a minimum of support. Maximum width of the groove is 7.5 cm; maximum depth, 3.5 cm (see Halffter, 1977, Fig. 13).

This nest is cared for by the female for about 40 days. She makes no attempts to destroy it but, rather, spends most of her time in the groove, cleaning and maintaining it. Development lasts about 43 days to teneral adult and another eight days to emergence. The female abandons the nest shortly before emergence and about a month later re-initiates a new period of ball-making. This 30 day period is about the same that passes between emergence of the adult and the beginning of its first nuptial feast; however, much longer times can elapse before it is begun.

Once inseminated, females can proceed with successive experimental and definitive nesting in the absence of a male.

When several females engaged in the nuptial feast occur in the same terrarium, a strong competition for space ensues. Each female tries to isolate her balls from other females, which may attack and eat them. Occasionally, fights occur for possession of balls in which each grapples with the other while lying on her side.

DISCUSSION

Undoubtedly, behavior of *Eurysternus* adults isolates this taxon from the two main evolutionary lines of feeding-nesting behavior of the scarabaeines (see Halffter, 1977). Although the species comprising the genus are morphologically uniform, the few species studied suggest two very different patterns of nesting behavior. Adults of the species described here, as well as those of *E. mexicanus*, display a complex nesting behavior designated Group VI by Halffter (1977). Another much simpler behavior is displayed by *E. foedus,* Guérin-Méneville and a Mexican species (see discussion below). The characteristics of Group VI, as illustrated by those species considered above are the following:

1) Balls are made only by females during the nuptial feast, the first phase of an elaborate nesting procedure. Moreover, most are made in large numbers and not rolled.

The nesting behavior of eurysternines, unlike that of scarabaeines, cannot be considered a derivative of feeding behavior. There are long periods during which feeding occurs but no ball-making, and there is direct feeding from a dung mass even though balls have been constructed. Balls can, however, be eaten. The fact that a large number of balls are made and left on the surface near the dung source (as opposed to being rolled away and buried as is done by Scarabeini) means that *Eurysternus* does not profit from the competitive advantages of rolling behavior; namely, less aggregation and more efficient use of resources. Ball-making by *Eurysternus* is, rather, a process related only to reproduction and which is correlated with a certain stage of ovarial development.

2) Nests are multiple. A multiple nest is a group of brood balls, each with an egg, where development takes place. Multiple nests cared for by parents (particularly the female) have arisen three different times, presumably independently, in Scarabaeinae. Although there are similarities in form and care, of the nest in each group, the way in which each is prepared is completely different.

In Group III (see Halffter, 1977) a male and female construct an underground chamber into which dung is brought and from which a female constructs brood balls. In Group V, a multiple nest arises from an addition of single balls rolled from a dung source and modelled independently. In *Eurysternus*, the balls comprising the nest are "selected" from a larger number prepared during the nuptial feast. Moreover, there are other differences. Females of Group III prepare a single nest where larval-pupal development is very long; fecundity is very low. In Groups V and VI, each female prepares several nests (*Eurysternus* females prepare several definitive nests) with intermediate periods of feeding. Even though a male may participate in nesting in all three groups, it is much more significant in Group III and non-existent in the definitive nests of *Eurysternus* (Group VI).

Nevertheless, the most distinctive feature of multiple nests of *Eurysternus*, and exclusive to them, are the experimental nests, which occur to various degrees in the three species studied here. Nothing even similar to experimental nests are known in other scarabaeines.

3) Nesting behavior follows the sequence a) nuptial feast, b) experimental nesting, c) definitive nesting. Females of *E. magnus* do not build experimental nests. But in *E. caribaeus*, *E. magnus* and *E. mexicanus* (Halffter, 1977) experimental and definitive nests are craters containing several brood balls. In *E. balachowskyi* the experimental nest is a crater, but the definitive nest is not (see above). When the brood balls are covered and united with soil by female *E. caribaeus*, the definitive nest is established. Care of a definitive nest is similar, but more elaborate by females of *E. balachowskyi*. Even though covered by a layer of soil, the brood balls of *E. magnus* and *E. mexicanus* are not united by soil and the balls are continually turned during care. Temporary care of experimental nest balls by *E. balachowskyi* females also includes periodic turning.

Our studies of *E. caribaeus* show that the state of ovarial development is linked with reproductive behavior. Maturation of a series of oöcytes coincides with nuptial feast; copulation determines termination of vitellogenesis, beginning of oviposition, and nest preparation. Nevertheless, unlike other scarabaeines, there is poor synchronization between ovarial development and nesting behavior. Our belief is that experimental nesting is attributable to a continuation of oocyte formation and maturation after a nest has been established. Thus, a female is influenced by contradictory signals: nesting behavior tends to promote continuance of nest care, while ovarial function promotes the construction of a new nest. Once the two signals come into phase, they reinforce each other (which may take an extended period of time), and definitive nesting ensues. If our hypothesis is true, formation of oöcytes must be slowest and more staggered in *E. magnus* and most rapid and unrelenting in *E. balachowskyi* and *E. mexicanus*.

If we suppose that reproductive behavior of scarabaeines in general tends toward being a K–strategy, the strategy is somewhat maladjusted in *Eurysternus* as compared to other known groups in that much reproductive effort is lost as a result of experimental nesting.

Since a male joins a female during preparation of nuptial balls, the latter behavior can be interpreted as a signal to a male that a female is physiologically prepared for copulation and oögenesis. Perhaps also a large number of nuptial balls is a better inducement for the male's parental investment than a small number, as a sort of proof of the female's nidificatory prowess. Thus, the nuptial feast may be the result of Darwinian sexual selection (in this case exercised by the male) in favor of advancing the usual nidificatory ball-making process to a period long preceding actual nidification. Transition between the early nuptial stage, favored by sexual selection, and the definitive nesting stage, favored by natural selection, can apparently be somewhat indefinite and confused in some species, since it is not in itself subject to any direct selection pressure. The resultant wastefulness of this intermediate experimental stage is presumably not sufficient to offset the combined selective advantages of the first and last stages.

Nesting behavior described so far is not universal to *E. foedus* and a yet unidentified Mexican species nest in a completely different manner. Females of these species bury shallowly a compact mass of excrement into which several eggs are laid. Larvae develop freely without encountering each other or moving around much. The dung mass later contains two or three tubular spaces created by the developing progeny. Among other differences, there is no ball-making or nest crater. This nesting pattern is remarkably like that of *Onitis caffer* Boheman and *O. aygulus (F.)*, which Halffter and Matthews (1966) assigned to Group I. Such behavior, which Halffter and Matthews (1966) considered an evolutionary antecedent to multiple nests, is no more characteristic of *Onitis* (and Onitini in general) than it appears to be for *Eurysternus*. How common it may be to *Eurysternus* remains to be seen.

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